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Natural Resource Stewardship and Science

Insect Pollinators of Denali National Park and Preserve

A Survey of Bees (Hymenoptera: Anthophila) and Flower Flies (Diptera: Syrphidae)

Natural Resource Report NPS/DENA/NRR—2015/952

ON THE COVER
Bumble bee (*Bombus* sp.) on *Hedysarum* flowers.
Photograph courtesy of Jessica Rykken, Harvard University

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Data in this report were collected and analyzed using methods based on established, peer-reviewed protocols and were analyzed and interpreted within the guidelines of the protocols.

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Abstract

Insect pollinators, specifically bees (Hymenoptera: Anthophila) and flower flies (Diptera: Syrphidae), are critical to maintaining healthy plant communities and functioning ecosystems in Denali National Park and Preserve. Despite their ecological importance and potential vulnerability to environmental threats such as climate change, the diversity of these pollinators has remained largely unknown to park scientists and managers. In an effort to establish a pollinator database, I conducted a survey in 2012 with three main objectives: (1) to document bee and flower fly diversity and distribution across selected areas of the park; (2) to provide information on habitat and plant community associations for individual species; and (3) to engage in outreach activities and create educational products to inform park staff and visitors about insect pollinators. In 2012, between June 21 and July 22, I used an insect net, bee bowls, and vane traps to collect bees and flower flies at 57 sites along the Denali Park Road. Sites were located between the eastern park entrance and Kantishna, approximately 148 km to the west; elevations ranged from 472 to 1480 m. I targeted early successional habitats, including gravel bars, and areas of high plant diversity, such as alpine tundra. A cooler and wetter than average growing season resulted in low pollinator activity. In all, I collected 552 bees comprising 20 species; the vast majority of bee specimens were bumble bees (*Bombus*; 502 specimens, 13 species). Flower flies were comparatively more diverse (42 species) even though fewer specimens (328) were collected. While many generalist pollinator species were collected in multiple habitats at various elevations, some species were primarily associated with lower or higher elevations (e.g., all solitary bees were collected down near the park entrance). Of special note, a flower fly species new to science in the genus *Cheilosia* was found near the East Fork cabin. I also documented the presence of the bumble bee, *Bombus occidentalis*, in the park, a western species that has been in drastic decline in the southern portion of its North American range. Park visitors and staff learned more about Denali's pollinators through activities such as a Denali-ology seminar, slide presentations, and weekly "open house with a researcher" sessions in the Murie Science and Learning Center. Pollinator fact sheets and website content are also in production for educating various audiences.

Acknowledgments

Funding for this project was generously provided by a Researcher-in-Residence grant from Denali NPP. With its emphasis on both science and outreach, this type of grant should serve as an excellent model for parks across the U.S. interested in supporting research into the lesser known realms of biodiversity.

I am especially grateful to Sierra McLane, NPS Education Coordinator at the Murie Science and Learning Center (MSLC), and Lucy Tyrrell, Research Administrator for Denali, both of whom helped me with all manner of logistics for living and working in the park, and enthusiastically supported the pollinator project. During my entire stay, the MSLC was a hive of activity with NPS staff, Alaska Geographic staff, interns, volunteers, researchers, and students, and their combined enthusiasm, knowledge, and interest to learn new things all contributed to my immense enjoyment of the people and landscapes of Denali.

As any entomologist knows, most of the work involved in an insect survey is back in the lab, sorting, pinning, labeling, and identifying specimens. I owe many thanks to Chris Thompson for contributing his time and expertise to identify all of the flower flies in his lab at the Smithsonian Institution in Washington, D.C, and also to Jamie Strange and Terry Griswold at the US Department of Agriculture Agricultural Research Service (ARS) Bee Biology and Systematics Lab in Logan, Utah for confirming my identifications and making determinations for a subset of bees.

Finally, thanks to the Denali bus drivers, unique characters whose love and appreciation of Denali wilderness and wildlife is deep and infectious, and who got me where I needed to go.

Introduction

The vast majority of flowering plants rely on animal pollinators for successful reproduction (Ollerton et al. 2011), and insects are by far the most diverse component of the pollinator fauna worldwide (Proctor et al. 1996). Among insects, bees (Hymenoptera: Anthophila) and flower flies (Diptera: Syrphidae) are important pollinator taxa, and both groups are relatively diverse and abundant in subarctic climates. In Denali National Park and Preserve (Denali), bees and flower flies are critical to maintaining healthy plant communities and functioning ecosystems, pollinating many of the plants that vertebrate herbivores and omnivores depend on for survival.

Pollinators are known to be at risk from various environmental threats such as habitat loss and alteration, invasive pollinator and plant species, parasites and pathogens, pesticides, and climate change (Potts et al. 2010). Declines have been well-documented and publicized for honey bees (Natural Research Council 2006), but have also been seen among native bumble bees (Cameron et al. 2011) and solitary bees (Burkle et al. 2013). Comparatively scant literature exists on the status of flower flies, although changes in species richness and composition pre-and post-1980 have been documented in Europe (Biesmeijer et al. 2006).

In a vast, protected subarctic wilderness such as Denali, changing climate is likely the prevailing threat to pollinator communities, with potential consequences including range shifts, decoupling of plant-pollinator networks, and species declines (Bartomeus et al. 2011, Cameron et al. 2011, Franzén and Öckinger 2012). In the face of such unprecedented threats, establishing a database of pollinator diversity in various habitats within Denali, especially in those habitats that are potentially vulnerable to effects from climate change (e.g., alpine tundra) is essential, both for a better understanding of current species composition and distributions within park and as a comparative baseline for monitoring changes in the future.

At a more basic level, all national parks are mandated by the National Park Service (NPS) Organic Act of 1916 to conserve the natural resources and wildlife on their lands for the enjoyment of future generations, yet most national parks know very little about the full suite of biodiversity that exists within their boundaries (Ginsberg 1994). For instance, Denali boasts a vast natural wilderness, and has been at the forefront of research in studying its wolves, bears, caribou, sheep and other vertebrates. However, as for all but a handful of national parks (e.g., Great Smoky Mountains, Boston Harbor Islands), the diversity, distribution, and abundance of the park's remaining 95% of non-microbial biodiversity, namely, the invertebrates, remains relatively unknown. Increasingly, there is an awareness that if park biologists and managers are expected to protect all wildlife within park boundaries now and into the future, as well as the functioning ecosystems of which they are integral components, then a better understanding of invertebrate biodiversity is essential (Ginsberg 1994).

Admittedly, it is not only the park that lacks data on pollinators. Information on bee and flower fly diversity and distribution in Alaska is scarce, given the immense area. Bishop and Armbruster (1999) reported 58 species of solitary bees and 18 species of bumble bees from the interior, and Pampel (2010) surveyed bumble bees near interior agricultural lands, documenting 17 species in all. Koch and Strange (2012) collected bumble bees along major transportation corridors from northern to southern Alaska and documented at least nine species, although they were focusing on just two species (*Bombus moderatus* and *B. occidentalis*) to analyze associated fungal pathogens. Habitat and plant associations for 41 species of solitary bees of interior and arctic Alaska were recorded by Armbruster and Guinn (1989). For flower flies, there is even less information available. Vockeroth (1992) listed 63 species recorded from Alaska in the Syrphinae, one of the two largest subfamilies of the Syrphidae, but there is no published estimate for the species richness of the other large subfamily, Eristalinae.

A general goal of the present survey was to build on what is known of the Alaska bee and flower fly fauna, and in particular, to focus on the diversity, distribution, and habitat associations of Denali's pollinators. It would be logistically impossible and very inefficient to sample across all of Denali's six million acres, so the survey focused on particular habitats known to be productive for pollinators and their host plants (e.g., alpine tundra, gravel river bars) in areas accessible from the park road. Specifically, the primary objectives were to:

(1) Inventory the bee and flower fly fauna of selected habitats in Denali NPP

(2) Document plant and habitat associations for identified species where possible

(3) Foster enthusiasm and appreciation of Denali's pollinators in park visitors and staff by engaging in activities and creating products for outreach and education.

An additional objective incorporated into the survey was to participate in a nationwide NPS-US Geological Survey (USGS) project (Multiregional evaluation of pollinator response to climate change in critical habitats service-wide, PMIS # 160800) comparing bee communities in habitats suspected to be most vulnerable to effects from climate change to those in less threatened habitats. In Denali, this entailed establishing paired transects in higher elevation alpine tundra and lower elevation shrub tundra that would be sampled in 2012 and 2013. Results from this study are not presented in this report.

Methods

Study Area

Denali comprises more than six million acres (approx. 2.46 million ha) in subarctic Alaska. Predominant habitat types include taiga forest at lower elevations in the eastern end of the park, wet and dry tundra above treeline with thick shrub cover below and alpine meadows above, boggy wetlands and braided rivers, rocky slopes and ridges, and at the highest elevations, the snow-covered peaks and glaciers of the Alaska Range. Tree line is generally at about 850 m on north-facing slopes, and up to 1100 m on south-facing slopes (Denali Fact Sheet, “Treeline shifts in Denali: influences of climate change and local site conditions”).

The park road runs east to west for nearly 150 km, parallel to the Alaska Range, beginning in the east at an elevation of approximately 475 m and reaching its highest point at Highway Pass, mile 59 on the road, at more than 1200 m. The western end of the road passes by Wonder Lake and ends in Kantishna, both at 500–600 m elevation. For this pollinator survey, beyond park headquarters at mile 3, I used the road for access to all sampling sites, and limited the study area to sites within approximately 5 km north or south of the road (Figures 1 and 2).

The flowering season in this subarctic system is relatively short, and variable between locations and years, depending on factors such as the severity of the winter, snow melt, exposure, and elevation. Typically, the main blooming season is between late-May and early August.

Collecting Pollinators

Between June 21 and July 22, 2012, I sampled pollinators in 57 locations within 5 km north or south of the park road, between Friday Creek Camp to the west, and Riley Creek Campground to the east (Figures 1 and 2, Table 1). Focal habitats included areas with floral blooms in: alpine tundra, alpine rocky areas, stream edges, river gravel bars, lower elevation meadows, shrub tundra, trailsides, and roadsides (Table 1).

Because almost all species of bees and flower flies need to be examined with a microscope to determine their identity, it was necessary to collect voucher specimens. The survey employed three methods for collecting insect pollinators: aerial nets, bee bowls, and blue vane traps. Nets allow active sampling of insects while they are in flight, feeding at flowers, or landed elsewhere. Netted specimens were killed with ethyl acetate in collecting jars.

Bee bowls and vane traps are passive trapping methods that attract pollinators with color (mimicking floral blooms). Bee bowls were set out in transects, with a small sign explaining the purpose of the cups and a brief description of the project at either end. Each 145 m-long transect comprised 30 plastic cups (Solo® 3.25 oz.;https://www.solutionsbysolo.com/Product/Sku/P325-0100), 10 blue, 10 yellow, and 10 white. The cups were spaced 5 m apart, and were filled approximately 3/4 full with a solution of 2 L water mixed with a few drops of detergent (Dawn® dish soap) to break the surface tension of the water. In areas with thick vegetation (e.g., *Vaccinium*) some bowls were elevated on 60 cm tall wire plant props so as to be visible to pollinators. Bee bowl transects were generally set out by 10 am and kept open for six or more hours, ensuring that they were open during the warmest part of the day, when bees are most actively foraging. At the end of the day, contents (i.e., drowned insects in soapy water) of all 30 bowls from a transect were poured into an 80 mm diameter tight-mesh kitchen strainer. The pooled insect catch from all bowls was then transferred from the strainer into a 4 oz. Whirl-Pak® via a wide-necked plastic funnel. Ethanol (95%) and a locality label were added to the contents before sealing shut the Whirl-Pak®.

Vane traps were of the type sold by Spring Star, Inc. (http://springstar.net/vanetrapblue.html). Each trap consisted of a 64 oz. plastic jar with a blue 15 cm diameter screw cap funnel, and two 24 cm (l) x 13 cm (w) blue plastic cross vanes attached in the top of the funnel. A piece of Dichlorvos (Vapona ®) fumigant strip is inserted into the jar to kill the captured insects. Vane traps were attached to plastic posts approximately 1 m above the ground, oriented sideways to keep out rain. Typically, one vane trap was located at each end of a bee bowl transect, and the contents of the two traps combined for one sample. Occasionally, single vane traps were set out without bee bowls and left for multiple days between collections.

Habitat and Floral Data

At each site, I recorded the general habitat type as well as the dominant plants in bloom. All but the most commonly encountered plants were photographed for later identification. Plants were identified to species where possible, using Pratt and Pratt (1993) as the primary reference, and later grouped into genera for association with habitats. A few sites are missing plant data due to time constraints in the field and/or poor images which did not allow identification.

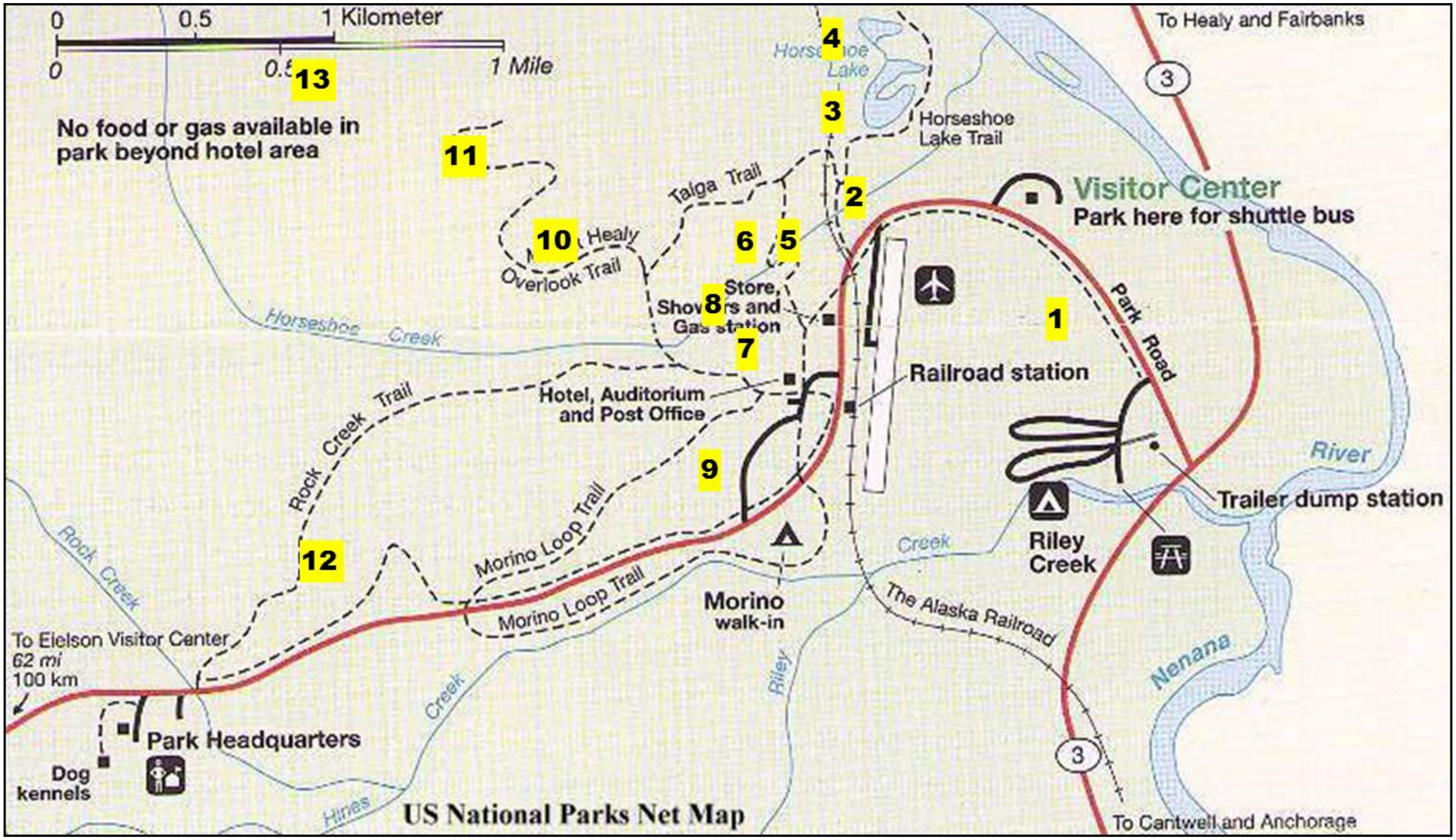

Figure 1. Approximate locations for pollinator sampling sites 1-13 (see Table 1) located in the eastern entrance area of Denali National Park and Preserve. For location of this area relative to rest of park, see Figure 2. (Map source: http://www.denali.national-park.com/map.htm)

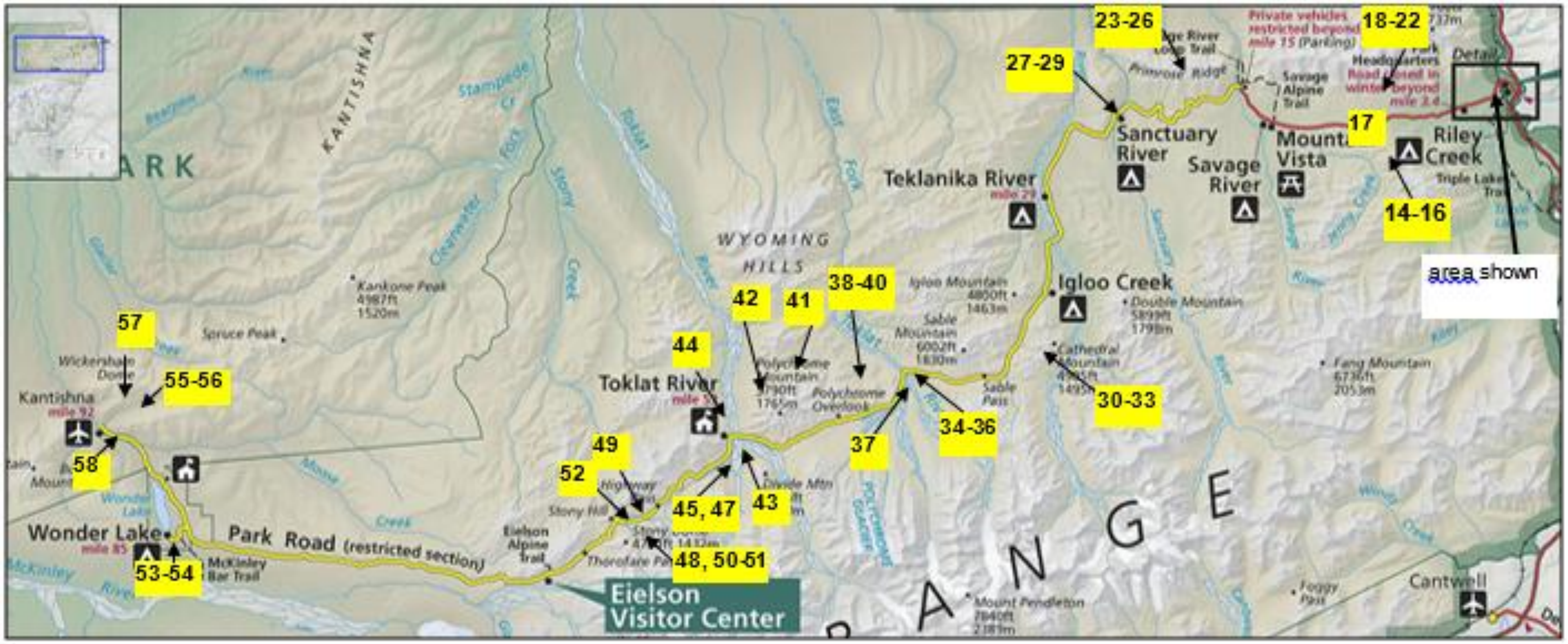

Figure 2. Approximate locations of pollinator sampling sites 14-58 (see Table 1; note there is no site 46) along the park road in Denali NPP. For detail in eastern park entrance area (sites 1-13), see Figure 1. (Map source: http://www.nps.gov/dena)

Table 1. Location, elevation, and general habitat description for 57 (#46 is eliminated) pollinator sampling sites in Denali NPP. Date of one or more collecting methods for each site is also shown. Sites in bold (#19, 22) were established for multi-seasonal sampling as part of a nationwide NPS bee survey project (see Introduction).

Site #	Sample location	Latitude	Longitude	Elev. (m)	Habitat	Net	Bowl	Vane
1	E. park entrance area; roadside near Riley Creek	63º 44' 18.85"	148º 53' 45.06"	497	roadside	6/23		
2	E. park entrance area; bike trail between MSLC and WAC	63º 43' 55.24"	148º 54' 29.02"	702	roadside	6/28, 7/4		
3	E. park entrance area; along Horseshoe Lake trail	63º 44' 32.53"	148º 54' 29.30"	472	trailside	6/27		
4	E. park entrance area; meadow/stream at Horseshoe Lake	63º 44' 35.23"	148º 54' 40.54"	475	lower meadow		7/14	7/14
5	E. park entrance area; park road and RR xing	63º 44' 12.44"	148º 54' 53.53"	544	roadside	7/14		
6	E. park entrance area; trails near yurt	63º 44' 07.66"	148º 55' 03.97"	552	trailside	6/21		
7	E. park entrance area; trail between MSLC and DVC	63º 43' 56.42"	148º 55' 04.04"	583	roadside		7/5, 7/13, 7/19	7/5, 7/13
8	E. park entrance area; roadside near MSLC	63º 43' 56.46"	148º 55' 08.54"	551	roadside		7/22	
9	E. park entrance area; Morino trail--old park roadbed	63º 43' 39.97"	148º 55' 10.92"	555	trailside	7/4, 7/15	7/6, 7/14, 7/15	7/6, 7/14-15
10	E. park entrance area; lower end of Healy Lookout trail	63º 44' 09.02"	148º 55' 55.70"	629	trailside	7/14	7/14	7/14
11	E. park entrance area; Healy Lookout trail below treeline	63º 44' 23.75"	148º 56' 41.68"	824	trailside	6/23		
12	E. park entrance area; roadside trail near HQ	63º 43' 26.40"	148º 56' 49.88"	635	roadside	6/22, 6/27	6/22	6/22
13	E. park entrance area; Healy Lookout trail above treeline	63º 44' 36.38"	148º 57' 14.44"	1090	alpine tundra	6/23		
14	Mile 7; S. side of road, up on ridgeline	63º 41' 15.11"	149º 03' 47.59"	1349	alpine tundra	7/22		
15	Mile 7; going up N-facing slope to high meadow	63º 41' 39.48"	149º 04' 18.80"	1147	alpine tundra	7/22		
16	Mile 7; on lower E-W ridge between high ridge and road	63º 41' 56.40"	149º 05' 38.83"	1111	alpine tundra	7/22		
17	Hines Cr.; roadside at base of hill	63º 42' 46.19"	149º 05' 54.82"	874	roadside	6/29		
18	Hines Cr.; near Hines Creek	63º 43' 15.10"	149º 07' 34.21"	1016	shrub tundra	6/29		
19	**Hines Cr.; Common lower site**	63º 43' 18.30"	149º 07' 37.81"	1025	shrub tundra		7/5-6, 7/19-20	7/5-6
20	Hines Cr.; shrubs between NET-13 and 15	63º 43' 48.97"	149º 07' 42.06"	1098	shrub tundra	6/29		
21	Hines Cr.; future VUL site	63º 44' 22.34"	149º 07' 50.27"	1202	alpine tundra	6/29		
22	**Hines Cr.; Vulnerable alpine site**	63º 43' 48.00"	149º 07' 50.27"	1240	alpine tundra	7/6	7/5-6, 7/19-20	7/5-6
23	Primrose; headed up the ridge; wet pockets	63º 44' 49.27"	149º 21' 07.63"	1407	alpine tundra	7/17		
24	Primrose; headed up the ridge	63º 44' 03.59"	149º 21' 37.33"	1096	alpine tundra	7/17		
25	Primrose; Mount Margaret	63º 45' 10.04"	149º 22' 07.03"	1487	alpine tundra	7/17		
26	Primrose; west of Mt. Margaret	63º 44' 58.27"	149º 23' 02.22"	1421	alpine tundra	7/17		
27	Sanctuary R.; on vegetated gravel bar north of bus stop	63º 43' 29.17"	149º 28' 19.16"	760	river gravel bar	7/17	7/18	7/18
28	Sanctuary R.; along road into campground	63º 43' 21.86"	149º 28' 19.56"	762	roadside		7/17	
29	Sanctuary R.; open area next to river, near campground	63º 43' 17.65"	149º 28' 29.17"	762	river gravel bar		7/17	7/17-18

Table 1 (continued). Location, elevation, and general habitat description for 57 (#46 is eliminated) pollinator sampling sites in Denali NPP. Date of one or more collecting methods for each site is also shown. Sites in bold (#19, 22) were established for multi-seasonal sampling as part of a nationwide NPS bee survey project (see Introduction).

Site #	Sample location	Latitude	Longitude	Elev. (m)	Habitat	Net	Bowl	Vane
30	Cathedral Mtn.; E-facing slope to rocky ridgeline	63º 33' 42.16"	149º 36' 41.54"	1420	alpine tundra	7/18		
31	Cathedral Mtn., descending drainage westwards	63º 33' 50.87"	149º 36' 52.96"	1273	alpine/rocky	7/18		
32	Cathedral Mtn.; steep dry slope with gravel patches	63º 33' 19.91"	149º 38' 06.43"	1171	alpine/rocky	7/18		
33	Cathedral Mtn.; down near creek by road/Sable Pass	63º 33' 22.28"	149º 38' 29.65"	1072	stream edge	7/18		
34	East Fork; around cabin and up along road east of bridge	63º 33' 27.50"	149º 46' 55.13"	942	roadside	7/8		
35	East Fork; creek bed alongside cabin	63º 33' 27.50"	149º 46' 55.13"	942	stream edge		7/9	7/9
36	East Fork; spur road into cabin	63º 33' 30.53"	149º 47' 07.37"	950	roadside		7/9	7/9
37	East Fork; west gravel bar of East Fork, south of bridge	63º 33' 17.46"	149º 47' 35.88"	935	river gravel bar	7/8	7/9	7/9
38	East Fork; E-facing slope between river and Polychrome	63º 33' 07.34"	149º 48' 29.45"	1185	alpine tundra	7/9		
39	East Fork; W-facing slope between river and Polychrome	63º 33' 11.95"	149º 48' 53.96"	1227	alpine tundra	7/9		
40	East Fork; W-facing ridge, heading to road	63º 32' 45.74"	149º 49' 08.26"	1221	alpine tundra	7/9		
41	Cabin Peak; saddles and drainage N of Polychrome	63º 31' 12.00"	149º 57' 55.51"	1043	alpine tundra	7/11		
42	Toklat; drainage from Polychrome into Toklat	63º 32' 38.98"	150º 01' 06.64"	976	river gravel bar	7/11		
43	Toklat; just south of bridge on Toklat	63º 31' 05.45"	150º 02' 39.12"	942	river gravel bar			7/1
44	Toklat; vegetated gravel bar near road camp	63º 31' 30.07"	150º 02' 45.71"	927	river gravel bar	6/30	6/30	6/30, 7/1,3-12
45	Toklat; west branch? Vegetated terrace on gravel bar.	63º 30' 16.63"	150º 02' 46.03"	972	river gravel bar		7/2	7/2
47	Toklat; gravel bars on west side of river	63º 30' 12.67"	150º 02' 53.20"	975	river gravel bar	6/30, 7/2		
48	Highway Pass; near Stony Dome	63º 27' 19.33"	150º 08' 50.89"	1480	alpine/rocky	7/1		
49	Highway Pass; meadow north of road	63º 28' 49.62"	150º 08' 52.01"	1256	alpine tundra	7/2	7/2	7/2
50	Highway Pass; loop around drainages	63º 24' 03.60"	150º 09' 34.13"	1202	alpine tundra	7/2		
51	Highway Pass; lower down, nearer road	63º 27' 42.05"	150º 09' 48.13"	1227	alpine tundra	7/1		
52	Highway Pass; roadside	63º 28' 04.08"	150º 10' 24.74"	1108	roadside	7/1		
53	Wonder Lake; south of road into campground	63º 27' 16.56"	150º 51' 10.76"	630	roadside		7/7	7/7
54	Wonder Lake; along road into the campground	63º 27' 16.34"	150º 51' 39.24"	612	roadside	7/7		
55	Kantishna; near pass on mining road (upper)	63º 32' 38.40"	150º 56' 19.50"	880	roadside	6/25		
56	Kantishna; first part of mining road (lower)	63º 32' 18.60"	150º 58' 29.60"	585	roadside	6/25		
57	Kantishna; trail up to Wickersham ridge	63º 32' 38.76"	150º 58' 46.56"	669	trailside	6/24,25		6/25
58	Kantishna; roadside near Friday Creek Camp	63º 32' 20.54"	150º 59' 08.02"	490	roadside	6/24,25		

MSLC=Murie Science and Learning Center, WAC=Wilderness Access Center, DVC=Denali Visitor Center.

Sample Processing and Specimen Identification

Specimens collected dry in nets were pinned in the field if logistics permitted, or back at the Murie Science and Learning Center (MSLC). Wet specimens from bee bowls, as well as those from vane traps, were stored in ethanol in Whirl-Paks® as explained above. I briefly trained several staff and volunteers at the MSLC to sort bee bowl samples to taxonomic order, and to pull out bumble bees. After this preliminary sort, I looked over all samples and extracted any remaining bees and flower flies. All other arthropod "by-catch" (e.g., wasps, ants, other flies, beetles, true bugs, butterflies) was sorted to order and stored separately in ethanol vials. Bees were washed in soapy water and then blow-dried with a hand-held hairdryer according to methods described in The Handy Bee Manual, compiled by Droege et al. 2009. Due to time constraints, only a small proportion of sample processing was performed at the MSLC, the bulk of the (unsorted) samples were mailed back to the Museum of Comparative Zoology for further processing. Once pinned and labeled with locality information, all flower flies were given to F.C. Thompson for identification at the Smithsonian Institution. Prepared and labeled bees were determined by J. Rykken, using the following references: Stephen 1957, Milliron 1973, Thorp et al. 1983, Koch et al. 2012, Pampell et al. 2012; and the Discover Life website for bee identification http://www.discoverlife.org/mp/20q?search=Apoidea. A subset of especially difficult specimens were sent to bee specialists at the US Department of Agriculture (USDA) Agricultural Research Service (ARS) Bee Biology and Systematics Lab (BBSL) in Logan, UT (J. Strange for bumble bees, T. Griswold for solitary bees). Vouchers of all species identified by J. Rykken were also sent to the BBSL for confirmation.

Specimen Deposition

All specimens were assigned and labeled with ICMS catalog numbers (DENA 40002-40881) and an accession number (DENA-00630). A subset of specimens were deposited at the Smithsonian Institution and the remainder will be deposited at the University of Alaska Museum (UAM) at the University of Alaska Fairbanks.

Results

A total of 552 bees and 328 flower flies were collected between June 21 and July 22, 2012; these included 42 species of flower flies, and 20 species of bees (Table 2). Among the flower flies, five morphospecies (sp. 1,5,6,7A,7B) in the genus *Platycheirus* could not be identified because males were not collected. It is as yet unclear whether specimens in the morphospecies 7A and 7B represent two species, or two variants of the same species (they are treated as two species in this report). One flower fly specimen in the genus *Cheilosia* is recognized to be a species new to science. Among the bees, one male *Bombus* remained unidentified due to its poor condition, and several of the solitary bees were identified to genus only (*Lasioglossum* sp., *Nomada* sp.), or received tentative species names due to significant variation from the norm in some key characters (*Andrena* aff. *nigrihirta*, *Panurginus* aff. *ineptus*). All of the identified bee species collected are previously known from Alaska, but among the flower flies, there are several unconfirmed new state records (Table 2, bold).

The most commonly collected pollinators overall were the bumble bees, *Bombus frigidus*, *B. sylvicola*, and *B. mixtus*, with more than 100 specimens each. These three generalist species were collected at all elevations, and in most or all of the habitats sampled. Among flower flies, the most abundant and widespread species were *Sphaerophoria philanthus*, *Platycheirus peltatoides*, and *Parasyrphus tarsatus*. Commonly collected species (10 or more specimens) with more restricted distributions included: *Xylota notha*, a flower fly collected only at lower elevations, along trails and roads, and the solitary bees, *Panurginus* aff. *ineptus* and *Hylaeus annulatus*, with similar lower elevation and trail/roadside distributions (Table 2). At higher elevations, the bumble bee *B. polaris*, and the flower flies *Platycheirus* 7A and 7B were collected primarily in alpine tundra and on river gravel bars, while *B. moderatus*, *B. balteatus*, *B. neoboreus*, and *Platycheirus ciliatus*, were also restricted to higher elevations but found in a wider range of habitats (Table 2). Twenty-five species were represented by just one or two specimens, insufficient numbers for making habitat associations.

Sampling sites were not distributed evenly among habitats (Table 3). Alpine tundra and roadsides were sampled most intensively, while only a single lower meadow site and two stream edge sites were visited. Pollinator catches reflected this sampling bias. More than half of all bees were collected in alpine tundra and roadsides, with river gravel bars and trailsides yielding a further 32% of the bee catch. Among flower flies, 91% of all specimens came from these four habitat types. Species richness followed a similar pattern, roadsides yielded the most species of bees (10 *Bombus* and 4 solitary species), with alpine tundra and gravel bars having 12 and 10 species of *Bombus*, respectively. Among flower flies, roadsides and trailsides yielded by far the most species, while river gravel bars and alpine tundra were next in diversity. Solitary bees, as noted above, were almost exclusively collected along trailsides and roadsides (5 and 4 species, respectively) at lower elevations.

Collecting methods complemented each other and varied in their yield of pollinators. Active netting captured 525 specimens (368 bees, 157 flower flies); passive bee bowls collected 342 specimens (176 bees, 166 syrphids); and vane traps, just 12 specimens (8 bees, 4 syrphids). Notably, all but 2 of the 50 solitary and cuckoo bees (i.e., non-*Bombus*) were collected in bee bowls.

Table 2. Bee and flower fly species collected during 2012 pollinator survey in Denali NPP. Distribution indicates whether the species has a Nearctic (NEA) or Holarctic (HOL) distribution, and if Holarctic, from which continents it has been documented: AS = Asia; EU = Europe; NA = North America. The number of specimens collected, number of sites in which they were found, and elevational range of those sites is shown, as is the specimen distribution across habitats. Habitat codes are defined in Table 3. Syrphidae species in bold are unconfirmed new AK records.

Family	**Subfamily**	**Species**	**Distribution**	**Specim.**	**Sites**	**Elev. (m)**	**Habitat**						
				#	#		AT	AR	LM	RG	RS	SE	ST
DIPTERA													
Syrphidae	Eristalinae	*Cheilosia bigelowi* Curran	NEA	3	3	497-927				x	x		
Syrphidae	Eristalinae	***Cheilosia columbiae* Curran**	NEA	2	2	950-1185	x				x		
Syrphidae	Eristalinae	***Cheilosia laevis* (Bigot)**	NEA	4	2	972-1240	x			x			
Syrphidae	Eristalinae	*Cheilosia latrans* (Walker)	NEA	6	5	475-762			x		x		
Syrphidae	Eristalinae	***Cheilosia* new sp.**	?	1	1	950					x		
Syrphidae	Eristalinae	***Cheilosia rita* Curran**	NEA	1	1	583					x		
Syrphidae	Eristalinae	*Cheilosia yukonensis* Shannon	NEA	5	3	927-1202	x			x			
Syrphidae	Eristalinae	*Eristalis cryptarum* (Fabricius)	HOL: EU, NA	1	1	475			x				
Syrphidae	Eristalinae	*Eristalis flavipes* Walker	NEA	1	1	942					x		
Syrphidae	Eristalinae	*Eristalis hirta* Loew	NEA	5	1	555							
Syrphidae	Eristalinae	*Helophilus hybridus* Loew	HOL: EU, NA	1	1	629							
Syrphidae	Eristalinae	***Sericomyia nigra* Portschinsky**	HOL: AS, EU, NA	1	1	551					x		
Syrphidae	Eristalinae	*Volucella bombylans* Linnaeus	HOL: AS, EU, NA	2	2	551-1090		x			x		
Syrphidae	Eristalinae	***Volucella facialis* Williston**	NEA	1	1	975				x			
Syrphidae	Eristalinae	***Xylota notha* Williston**	NEA	22	5	551-635					x		
Syrphidae	Syrphinae	*Baccha elongata* (Fabricius)	HOL: EU, NA	1	1	635					x		
Syrphidae	Syrphinae	*Dasysyrphus amalopis* (Osten Sacken)	NE	5	5	472-1090		x			x		
Syrphidae	Syrphinae	*Dasysyrphus venustus* Meigen	HOL: AS, EU, NA	15	10	552-1227	x	x		x	x		
Syrphidae	Syrphinae	*Epistrophe grossulariae* (Meigen)	HOL: AS, EU, NA	2	1	555							
Syrphidae	Syrphinae	***Eupeodes americanus* (Wiedemann)**	NEA	1	1	824							
Syrphidae	Syrphinae	*Eupeodes curtus* (Hine)	HOL: EU, NA	10	6	555-1480	x	x					
Syrphidae	Syrphinae	*Eupeodes luniger* (Meigen)	HOL: AS, EU, NA	3	3	583-975				x	x		
Syrphidae	Syrphinae	*Megasyrphus laxus* (Osten Sacken)	NEA	9	5	552-824					x		
Syrphidae	Syrphinae	*Melangyna arctica* (Zetterstedt)	HOL: EU, NA	8	5	555-1043	x			x	x		
Syrphidae	Syrphinae	*Melanostoma mellinum* (Linnaeus)	HOL: AS, EU, NA	13	7	585-1202	x			x	x		x
Syrphidae	Syrphinae	*Meligramma triangulifera* (Zetterstedt)	HOL: EU, NA	3	3	555-635					x		
Syrphidae	Syrphinae	*Meliscaeva cinctella* (Zetterstedt)	HOL: AS, EU, NA	4	3	555-927				x			
Syrphidae	Syrphinae	***Neocnemodon rita* (Curran)**	NEA	1	1	555							
Syrphidae	Syrphinae	***Parasyrphus genualis* (Williston)**	NEA	3	2	824-1090		x					
Syrphidae	Syrphinae	*Parasyrphus tarsatus* (Zetterstedt)	HOL: AS, EU, NA	19	13	555-1487	x	x		x	x		
Syrphidae	Syrphinae	*Pipiza macrofemoralis* Curran	NEA	1	1	942						x	

Table 2 (continued). Bee and flower fly species collected during 2012 pollinator survey in Denali NPP. Distribution indicates whether the species has a Nearctic (NEA) or Holarctic (HOL) distribution, and if Holarctic, from which continents it has been documented: AS = Asia; EU = Europe; NA = North America. The number of specimens collected, number of sites in which they were found, and elevational range of those sites is shown, as is the specimen distribution across habitats. Habitat codes are defined in Table 3. Syrphidae species in bold are unconfirmed new AK records.

Family	**Subfamily**	**Species**	**Distribution**	**Specim.**	**Sites**	**Elev. (m)**	**Habitat**						
				#	#		AT	AR	LM	RG	RS	SE	ST
DIPTERA (cont'd.)													
Syrphidae	Syrphinae	***Platycheirus ciliatus* Bigot**	NEA	12	8	702-1240	x			x	x		x
Syrphidae	Syrphinae	Platycheirus obscurus (Say)	NEA	1	1	585					x		
Syrphidae	Syrphinae	*Platycheirus peltatoides* Curran	NEA	21	12	472-1240	x	x		x	x		x
Syrphidae	Syrphinae	*Platycheirus* sp. 1	?	4	3	555-975				x	x		
Syrphidae	Syrphinae	*Platycheirus* sp. 5	?	1	1	1016							x
Syrphidae	Syrphinae	*Platycheirus* sp. 6	?	2	1	1025							x
Syrphidae	Syrphinae	*Platycheirus* sp. 7A	?	11	4	972-1240	x			x			
Syrphidae	Syrphinae	*Platycheirus* sp. 7B	?	41	4	935-1240	x			x		x	
Syrphidae	Syrphinae	*Sphaerophoria philanthus* Meigen	NEA	61	16	490-1240	x			x	x		x
Syrphidae	Syrphinae	*Syrphus attenuatus* Hine	HOL: EU, NA	1	1	874					x		
Syrphidae	Syrphinae	*Syrphus ribesii* (Linnaeus)	HOL: AS, EU, NA	20	7	472-1025				x	x		x
HYMENOPTERA													
Andrenidae	Andreninae	*Andrena aff. nigrihirta* (Ashmead)	NEA	2	1	555							
Andrenidae	Andreninae	*Andrena rufosignata* Cockerell	NEA	1	1	555							
Andrenidae	Andreninae	*Panurginus aff. ineptus* Cockerell	NEA	20	4	551-635					x		
Apidae	Apinae	*Bombus balteatus* Dahlbom	HOL: EU, NA	31	17	760-1480	x	x		x	x		
Apidae	Apinae	*Bombus flavifrons* Cresson	NEA	55	21	551-1227	x			x	x	x	
Apidae	Apinae	*Bombus frigidus* Smith	NEA	113	33	475-1421	x	x	x	x	x	x	x
Apidae	Apinae	*Bombus hyperboreus* Schönherr	HOL: AS, EU, NA	2	1	1420	x						
Apidae	Apinae	*Bombus insularis* (Smith)	NEA	3	3	544-1185	x			x	x		
Apidae	Apinae	*Bombus jonellus* (Kirby)	HOL: AS, EU, NA	1	1	1043	x						
Apidae	Apinae	*Bombus melanopygus* Nylander	NEA	23	11	472-1147	x			x	x		
Apidae	Apinae	*Bombus mixtus* Cresson	NEA	103	26	475-1420	x	x	x	x	x	x	
Apidae	Apinae	*Bombus moderatus* (Linnaeus)	NEA	34	17	702-1420	x	x		x	x	x	x
Apidae	Apinae	*Bombus neoboreus* Sladen	NEA	21	14	702-1487	x	x		x	x	x	
Apidae	Apinae	*Bombus occidentalis* Greene	NEA	1	1	583					x		
Apidae	Apinae	*Bombus polaris* Curtis	HOL: AS, EU, NA	10	7	760-1421	x			x			
Apidae	Apinae	*Bombus sylvicola* Kirby	NEA	104	31	475-1487	x	x	x	x	x		x
Apidae	Nomadinae	*Nomada* sp.	?	1	1	555							
Colletidae	Colletinae	*Colletes impunctatus lacustris* Swenk	NEA	3	3	475-583			x		x		
Colletidae	Hylaeinae	*Hylaeus annulatus* (Linnaeus)	HOL: AS, EU, NA	22	3	551-583					x		
Halictidae	Halictinae	*Lasioglossum "Evylaeus"* sp.	?	1	1	583					x		

Table 3. Summary of habitats sampled for pollinators in Denali NPP, including: number of sites sampled; elevational range of sites; and total abundance and species richness of pollinators within each habitat.

Habitat	**Habitat** code	**# Sites**	**Elev. range** (m)	**# Specimens**		**# Species**	
				Bees	Syrphids	Bees	Syrphids
Alpine tundra	AT	17	1043-1487	166	79	12	13
Roadside	RS	16	490-1108	154	70	14	25
River gravel bar	RG	8	760-976	99	61	10	17
Trailside	TS	6	472-669	76	89	8	23
Alpine rocky	AR	4	1090-1480	29	14	3	7
Shrub tundra	ST	3	1016-1098	11	11	3	7
Stream edge	SE	2	942-1072	13	2	5	2
Lower meadow	LM	1	475	4	2	4	2

A diversity of flowering plants (58 genera) were recorded across all sites, and each habitat type was associated with several plant genera common to many or most of its sites (Table 4). There was some overlap of common plant genera between habitats (e.g., *Epilobium* and *Hedysarum* were both common in river gravel bars and along roadsides), but sometimes the species within these genera differed between habitats (e.g., river beauty, *Epilobium latifolium* was common along river gravel bars, while tall fireweed, *Epilobium angustifolium* was common along roadsides). Species-specific associations between pollinators and their hosts were not recorded (and not possible with passive traps), however casual observations while net collecting suggested that many *Bombus* species were feeding on a wide range of flowers, including those with long corollas, such as *Hedysarum* and *Mertensia*, complex flowers such as *Aconitum*, and open flowers such as *Potentilla*.

Table 4. Plant genera recorded in eight habitats across 57 pollinator sampling sites in Denali NPP. Site numbers correspond to those in Table 1. Shading indicates a genus that is commonly seen in that habitat (i.e., documented in a minimum of 2-5 sites, depending on the habitat). See Table 3 for habitat codes.

Site #	Habitat type	Achillea	Aconitum	Anemone	Arctostaphylo	Arnica	Aster	Astragalus	Boykinia	Campanula	Cassiope	Cardamine	Castilleja	Chrysopleniu	Claytonia	Cornus	Crepis	Delphinium	Dodecatheon	Draba	Dryas	Epilobium	Eritrichium	Gentiana	Hedysarum	Ledum	Linnea	Lloydia	Loiseleuria	Lupinus
14	AT					x					x										x									
15	AT			x		x			x		x																			
16	AT																													
21	AT		x					x			x				x				x		x	x								x
22	AT		x		x							x							x	x		x	x				x			x
23	AT		x					x		x											x			x						
24	AT		x			x																								
25	AT																													
26	AT		x												x															
30	AT										x							x			x									
38	AT					x															x				x					
39	AT										x														x					
40	AT					x																								
41	AT							x	x													x			x					
49	AT							x							x						x									
50	AT																													
51	AT																													
13	AR																				x									
31	AR																				x	x								
32	AR								x						x						x		x	x						
48	AR											x		x	x					x			x							
4	LM																					x								
27	RG						x	x																	x					
29	RG																					x			x					
37	RG						x	x									x					x			x					
42	RG							x														x								
43	RG																													
44	RG							x														x			x					
45	RG																													
47	RG							x									x					x			x					
1	RS																													
2	RS																													
5	RS																													
7	RS																													
8	RS	x											x									x								
12	RS				x											x						x			x	x				
17	RS																													
28	RS		x				x															x			x					
34	RS																					x			x					
36	RS																								x					
52	RS																								x					
53	RS																													
54	RS															x						x			x		x			
55	RS			x		x					x		x								x						x			
56	RS								x													x				x				
58	RS																					x								
33	SE																					x								
35	SE																								x					
18	ST			x												x								x						
19	ST		x	x											x	x								x						
20	ST																													
3	TS																													
6	TS																													x
9	TS	x	x			x	x	x								x		x				x			x					
10	TS		x													x						x			x		x			
11	TS		x															x												
57	TS		x										x					x						x				x	x	

Table 4 (continued). Plant genera recorded in eight habitats across 57 pollinator sampling sites in Denali NPP. Site numbers correspond to those in Table 1. Shading indicates a genus that is commonly seen in that habitat (i.e., documented in a minimum of 2-5 sites, depending on the habitat). See Table 3 for habitat codes.

Site #	Habitat type	*Minuartia*	*Myosotis*	*Oxytropis*	*Papaver*	*Parnassia*	*Parrya*	*Pedicularis*	*Polemonium*	*Polygonum*	*Potentilla*	*Pyrola*	*Ranunculus*	*Rosa*	*Rubus*	*Rumex*	*Salix*	*Saussurea*	*Saxifraga*	*Sedum*	*Senecio*	*Shepherdia*	*Silene*	*Solidago*	*Spiraea*	*Vaccinium*	*Valeriana*	*Zygadenus*
14	AT																		x							x		
15	AT	x								x								x								x	x	
16	AT															x												
21	AT				x			x									x										x	
22	AT								x	x							x											
23	AT	x		x	x			x		x										x	x						x	
24	AT																											
25	AT																											
26	AT									x																	x	
30	AT																			x	x		x					
38	AT									x	x												x					
39	AT																x									x		
40	AT			x			x										x								x			
41	AT							x			x																	
49	AT	x						x																		x		
50	AT																											
51	AT				x			x																				
13	AR																											
31	AR												x															
32	AR	x						x			x									x								
48	AR	x		x	x			x											x				x					
4	LM					x					x	x			x						x	x						
27	RG			x		x					x										x			x				
29	RG							x			x																	
37	RG																											
42	RG																							x				
43	RG																											
44	RG			x								x									x							x
45	RG																											
47	RG																											x
1	RS																											
2	RS																											
5	RS																											
7	RS																											
8	RS																											
12	RS										x			x														
17	RS																											
28	RS										x										x			x				
34	RS										x													x				
36	RS										x													x				
52	RS																											x
53	RS																											
54	RS																								x			
55	RS		x					x	x															x		x		
56	RS				x				x	x																		
58	RS																											
33	SE		x								x																	
35	SE										x													x				
18	ST							x		x															x	x		
19	ST							x													x				x	x		
20	ST																											
3	TS			x							x			x														
6	TS																											
9	TS			x										x							x			x				
10	TS																				x							
11	TS							x	x	x	x			x											x			
57	TS			x	x					x	x	x													x	x		

Discussion

Five weeks of sampling in unseasonably cool and wet weather were not sufficient to complete a comprehensive survey of pollinators in Denali, but the survey established a baseline database and laid the groundwork for future efforts.

Denali's Pollinators

Bumble Bees (Bombus species)

As expected, bumble bees made up the majority of bee species in the survey. Bumble bees are well-adapted to the adverse climates of high latitudes and altitudes because of their comparatively large body size; long, dense pelage; and ability to warm their thoracic muscles through "shivering" which allows them to fly at lower temperatures than most insects (Heinrich 1979, Bishop and Armbruster 1999, Kearns and Thomson 2001). Bumble bees are typically generalist foragers with relatively long tongues (although tongue length varies between species) and these traits are also beneficial in alpine/arctic systems where the flowering season is compressed.

Social bumble bees have nests which last for just one growing season (unlike honey bees, whose nests are perennial). Queens emerge from hibernation in the spring, nourish themselves with nectar and pollen before establishing a nest and foraging for their first brood, and then may remain in the nest producing more offspring as their workers assume the work of gathering more nectar and pollen. Later in the season, the queen produces males and virgin queens, and once mated, only new queens will overwinter in hibernacula, the rest of the colony dies. Bumble bees in the subarctic have adapted to completing this cycle in a relatively short time compared to their temperate counterparts. Vogt et al. (1994) studied six *Bombus* species in Denali, and found that queens were much quicker to begin foraging and establishing nests after emerging from dormancy than bumble bees in Vermont or New York. Measurements revealed that the development of their ovaries was also accelerated. At Camp Denali in Kantishna, the researchers noted activity of the first queens (*B. frigidus, B. balteatus, B. flavifrons, and B. sylvicola*) on the same day that the first willow blossoms opened, May 20, 1992. This is a full month earlier than my survey began in 2012. I noted queens of various species flying throughout the end of June and the first three weeks of July, but it was not possible to tell founding queens (born the previous year) from new queens (produced in 2012) based on appearance. The bulk of the total catch was comprised of worker (sterile) females, but among the most abundant *Bombus* species I also collected a significant proportion of males, with the exception of *B. neoboreus* (Figure 4). Males of *B. frigidus, B. melanopygus*, *B. mixtus*, and *B. sylvicola* were collected as early as the third week of June (when sampling began), suggesting that colony development for these species was well underway.

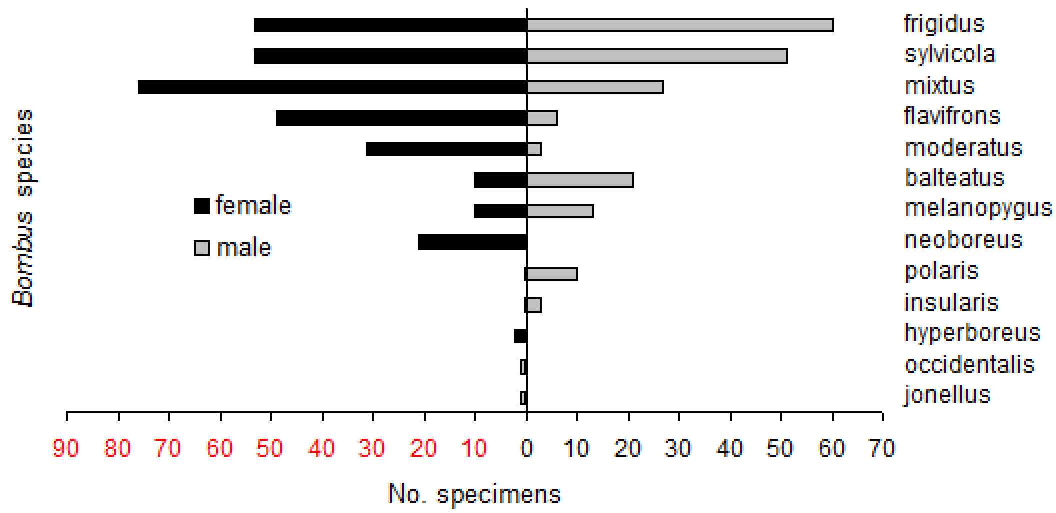

Figure 3. Number of *Bombus* females and males collected between June 22 and July 22, 2012 in Denali NPP.

In addition to social bumble bees, I documented two species of social parasites. *Bombus insularis* belongs to the subgenus *Psithyrus*, which includes most of the other obligate social parasites. These bees do not build nests of their own, nor do they have a worker caste. Instead, a female *Psithyrus* bee will invade the nest of a host (social) species, kill the queen, and usurp the nest, so that host workers will raise her young. Thus, female *Psithyrus* bees do not collect pollen and nectar for the nest, and have no special structures on their legs (corbiculae) for pollen transport. Known hosts for *Bombus. insularis* include *B. flavifrons* and *B. occidentalis* (Krombein et al. 1979). I also documented *Bombus hyperboreus*, which is an unusual species in that it belongs to the subgenus *Alpinobombus*, despite its parasitic lifestyle on other species of the same subgenus. Known hosts include *B. polaris* and *B. balteatus* (Krombein et al. 1979, Gjershaug 2009). Unlike *Psithyrus* species, *B. hyperboreus* does collect and transport pollen for the usurped nest, and thus has fully developed corbiculae.

Solitary and Cuckoo Bees

World-wide, by far the greatest bee diversity is found among solitary nesting and cleptoparasitic ("cuckoo") species (Michener 2000), however, as discussed above, in alpine/(sub)arctic systems, social *Bombus* dominate many habitats. Among the bees collected in Denali, fewer than ten percent of individuals, and just over one third of the species, were solitary or cuckoo species. These seven species represented six genera and four families. All of the solitary bees were found at lower elevations in the eastern end of the park, most were collected in bee bowls along a well-travelled path connecting the two visitor centers. Almost all of these species are ground nesters (except *Hylaeus*, which typically nests in twigs), requiring bare soil for excavating nests, and so disturbed/planted ground in the developed areas of the park may be serving as good habitat for these bees. I documented just one cuckoo bee, in the genus *Nomada*. Instead of building their own nests and gathering nectar and pollen to provision their young as female solitary bees do, cuckoo bees lay their eggs in the nest of a host bee (in the case of *Nomada*, host bees are often in the genus *Andrena*). Within each nest cell, the developing cuckoo larva kills the host egg or larva and eats their nectar and pollen provisions. The cuckoo lifestyle is not uncommon among bees, a summary of surveys conducted in various regions of the U.S. suggests that parasitic bees make up between 10 and 25% of bee faunas (Wcislo 1987).

Given the unusually cool, wet summer in 2012, it may be that solitary bees in other areas of the park were less active than in more typical years, and remained undetected. Armbruster and Guinn (1989) documented 41 species of solitary bees across 34 sites in interior and arctic Alaska. The majority of their bees came from grassy, south-facing bluffs, roadsides, and floodplains; only one site was located in alpine tundra. Bishop and Armbruster (1999) cited 58 species of solitary bees in interior Alaska, and noted they were restricted to warm, open habitats. More survey work in Denali at lower elevations and on south-facing exposures may yet reveal a richer fauna of solitary bees.

Flower Flies (Syrphidae)

I collected flower flies in two major subfamilies of the Syrphidae, Syrphinae and Eristalinae. Adults of both subfamilies visit flowers to feed on pollen and nectar, and thus effect pollination. Their mobile larvae, however, lead very different lives. Larval Syrphinae are predators, feeding mainly on aphids and other homopterans, and some have been used for biocontrol of aphid pests in agriculture. Larval Eristalinae are more varied in their habits. *Cheilosia* larvae feed on fungi or plant tissue; *Volucella* larvae are scavengers in the nests of social wasps (e.g., yellowjackets); *Eristalis*, *Helophilus*, and *Sericomyia* larvae live in stagnant, organic water (Vockeroth and Thompson 1987); and *Xylota* larvae are often associated with decaying wood.

As adults, flower flies are quite conspicuous while feeding on flowers, and their mimicry of stinging bees and wasps is believed to be a defensive strategy (Vockeroth and Thompson 1987). Among the syrphids collected in Denali, the most convincing bumble bee mimics are the two *Volucella* species and *Eristalis flavipes*, all large-bodied flies with relatively thick piles of yellow, orange, and/or black pile on their thorax and abdomen. *Volucella bombylans* is a widespread and polymorphic species, mimicking bumble bees local to its area (Marshall 2012).

I collected one flower fly species new to science in the genus *Cheilosia*. The single specimen was collected in a bee bowl, along the spur road leading into the East Fork cabin. *Cheilosia* is the most diverse holarctic genera within the Syrphidae (Vockeroth and Thompson 1987), and for most species whose biology has been studied, larvae develop within plant stems or fungus. A few *Cheilosia* species with larvae whose plant hosts are known have been used as biocontrol agents for invasive weeds (Grosskopf 2005). Denali's new pollinator species awaits formal description by F.C. Thompson and/or colleagues. Finding more specimens of this new species will be important for this effort.

Efficacy of Collecting Methods

All insect collecting methods have benefits and biases, and inventories are best accomplished using a combination of active and passive (i.e., trapping) approaches (Grundel et al. 2011). Net-collecting is the simplest method, and in this survey was used in all habitats, especially in remote sites such as alpine tundra and rocky ridges, far from the road. The drawbacks of netting include that it provides only a snapshot of what is active at the time of sampling, it is not easily repeatable, and, depending on the skill of the sampler, there may be a bias towards more obvious, larger, and/or slower insects.

Pan-trapping (in this case, "bee bowls") is a relatively simple passive collecting technique, and complements net-collecting by allowing a longer window of sampling, and is also easily repeatable by anyone, regardless of skill. On the down-side, bee bowls also have biases in their catch, and they are less ideal for remote sites because they must be set out and then collected several hours later, all the while vulnerable to disturbance from curious wildlife or park visitors. I sampled with bee bowls primarily in more accessible sites (24 transects in all), such as along roadsides, trailsides, and river gravel bars, but rarely in alpine tundra. Grundel et al. (2011) found that the most common species in their bee surveys were collected by both nets and bee bowls, but uncommon species were often only collected with one method or the other, and thus concluded that both netting and pan-trapping were necessary for a complete survey of diversity at their sites. In the Denali survey, almost three quarters of the bumble bees were collected by net, while more than half of the flower flies were collected in bee bowls. The small, uncommon solitary bees were almost all (48 out of 50) collected in bee bowls. Of 25 pollinator species for which only one or two specimens were collected overall, 14 species were collected only in bee bowls, and 8 only in nets.

Vane traps were the third method of trapping I employed, but they collected very few specimens. This is surprising, given the success of the method for a variety of non-honey bees, discovered serendipitously by Stephen and Rao (2005), and specifically for bumble bees in interior Alaska, employed by Pampell (2010). It is unclear why the traps were so unsuccessful in Denali, because care was taken to replicate techniques (e.g., killing agent, trap orientation) used successfully in previous studies. A Malaise trap had also been considered for this survey, primarily to collect flower flies. These are large, mesh, tent-sized barrier traps that are designed to intercept insects in flight. The logistics of carrying in and setting up this conspicuous trap, coupled with the risk of leaving it unattended with large, curious animals nearby, influenced my decision not to use it in this preliminary investigation.

The Relative Importance of Insect Pollinators in Denali

The dependence of plants on insects for pollination in arctic systems has been a topic of research and discussion among entomologists and botanists alike (Mosquin and Martin 1967, Hocking 1968, Kevan 1972). While plants have evolved many strategies for successful reproduction, including asexual reproduction, self-pollination, and wind pollination, insects are undoubtedly critical for the survival of many plant species in arctic and subarctic landscapes. Kevan (1972) showed with exclusion experiments on Ellesmere Island that *Salix arctica*, *Pedicularis capitata*, *Dryas integrifolia*, and *Saxifraga oppositifolia* (all plants found in Denali) were dependent on insects—including *Bombus* and flower flies—for successful seed set. Interestingly, he also found that *Epilobium latifolia* and *Cassiope tetragona*, both plants on which many *Bombus* were observed in Denali during the survey, did not rely on insects for seed set.

The relative contribution of different insect taxa to plant pollination also varies with latitude and altitude (Elberling and Oleson 1999). Among the focal taxa in this survey, bumble bees were noticeably more abundant, widespread, and active than solitary bees or flower flies. As generalist foragers with strong thermoregulatory capabilities, *Bombus* are ideally suited to foraging in more severe climates, and thus have an important role in alpine and subarctic pollination. Their densely hairy bodies are also very effective at transferring pollen between plants. Though super-diverse in more temperate climates, solitary bees, which often have more specialized associations with host plants, are also more limited by their thermal capacities in extreme climates (Armbruster and Guinn 1989, Bishop and Armbruster 1999). The contribution of flower flies as pollinators has received less attention than bees, but Bischoff et al. (2013) compared pollinator performance on two alpine herbs and found that a solitary masked bee delivered 3 to 10 times as much pollen to receptive stigmas as did a flower fly, though the two taxa made similar numbers of visits to the plants. Thus, per-visit effectiveness is important to consider in addition to visitation rate when comparing pollinator contributions. Flower fly species also likely vary in their pollen transfer effectiveness, with hairy eristaline species (e.g., *Bombus* mimics) probably carrying more pollen than relatively smooth flies.

Casual observations in Denali suggested that calypterate flies (generally dark-colored, robust flies comprising several related families) were far more abundant than either bees or flower flies on floral blooms throughout the duration of the survey. The domination of Diptera on arctic and alpine flowers is well-documented (Mosquin and Martin 1967, Kevan 1972, Elberling and Oleson 1999). Syrphids make up a small proportion, but other fly taxa which are known to visit flowers in abundance include: Anthomyiidae (root maggot flies), Muscidae (house flies and relatives), Calliphoridae (blow flies), Sciaridae (dark-winged fungus gnats), Chronomidae (non-biting midges), Phoridae (scuttle flies), and Empididae (dance flies; Elberling and Oleson 1999). An illustrative example is Levesque and Burger's (1982) study on insect visitors to *Minuartia groenlandica* on Mt. Washington in New Hampshire. Of 15 insect species observed visiting this alpine plant, 14 were flies (including two flower fly species), joined by just one species of bumble bee. Pollen loads varied widely among the species, with female *Bombus* carrying, on average, more than 13 times the pollen load of the most loaded non-flower flies. However, flies with relatively small pollen loads (e.g., muscids, anthomyiids) were active on cold, cloudy days when *Bombus* and syrphids were not observed to be visiting flowers, thus, the authors contended that their collective contributions to pollination were significant. In the Denali survey, non-focal taxa were not actively collected, but significant numbers of calypterate and other non-flower flies comprised "by-catch" in bee bowls. These specimens are currently stored in ethanol at the UAM, and are accessible for future study.

Habitat Requirements and Associations

Habitat needs for bees and flower flies include: host plants with nectar and pollen for adults (and bee larvae) to feed upon; various other food resources for flower fly larvae (e.g., aphids, plants stems, wood, fungus, organic water); and nesting substrate for bees (e.g., bare ground, twigs, abandoned rodent nests). Although one initial goal of the survey was to associate pollinator species with particular habitats and floral hosts within the park, the generalist habits and/or low abundances of many of the species (i.e., 37 species with $\leq$5 specimens) as well as inconsistent detail recorded for floral diversity at many of the sites, did not allow much confidence for making strong associations. However, information can be gleaned from the literature that provides insights into important habitat needs and likely associations for various pollinator taxa, with which I can compare my observations.

Almost all of the pollinator species documented in the survey are considered generalist foragers as adults, however, the structure of mouthparts can limit which types of flowers a species is able to access. Bumble bees, as a group, are classified as "long-tongued" bees, however, individual species vary significantly in tongue length, and this determines the depth of corolla tube they can access for nectar. For instance, species in the subgenus *Alpinobombus* (*B. polaris*, *B. balteatus*, *B. hyperboreus*, *B. neoboreus*) have medium to long tongues, and thus can access deep corollas (e.g., *Delphinium*), while species in the subgenus *Bombus* (*B. occidentalis*, *B. moderatus*) have relatively short tongues and can feed only on shallow flowers (e.g., *Dryas octopetala*, *Potentilla fructicosa*). Some short-tongued bees also "rob" nectar by chewing a small hole from the outside of the flower to reach the nectaries. The remainder of the bumble bees I collected have short to medium length tongues (tongue length information obtained from http://www.nhm.ac.uk/research-curation/research/projects/bombus/; accessed 10/24/2013). All the sampled habitats in Denali had a variety of flowers with both shallow and deep corollas, and it is unlikely that bumble bees were associated with particular habitats based on foraging needs. Among solitary bees, all identified species are known to be generalist feeders with the possible exception of *Colletes impunctatus lacustris*, which has been recorded on *Brassica* and possibly *Gaylussacia* (Krombein et al. 1979). As with bumble bees, tongue length (as well as body size) determines which flowers solitary bees can access for nectar and/or pollen (Armbruster and Guinn 1989). Flower fly adults consume nectar or pollen or both to fuel themselves, but do not feed their young. As with bees, proboscis length correlates with the corolla depth of nectar flowers (Gilbert 1981). Overall, flowers in the Apiaceae and Asteraceae are most favored by flower flies; interestingly, syrphids in the genera *Melanostoma* and *Platycheirus* feed on the pollen of wind-pollinated plants such as grasses (Proctor et al. 1996).

Nesting sites are a critical habitat component for bees. Bumble bees generally nest in abandoned rodent or other nests below ground, or on the ground surface. After emergence from hibernation, the queen searches for a suitable nest in a dry, sunny location, often on south-facing slopes (Kearns and Thomson 2001). Solitary bees in the genera *Andrena*, *Panurginus*, *Colletes*, and *Lasioglossum* typically excavate nests underground, and depend on relatively bare patches of well-drained soil for these nests. The landscaped/disturbed areas near trails and buildings in the park entrance area may be providing such habitat for mining bees. *Hylaeus* bees are generally twig nesters, and excavate the pithy stems of berry canes or shrubs. Unlike bees, flower flies do not build nests and provision their young, however, their larvae are active foragers and so larval food requirements (e.g., aphids, plants stems, water) are also important habitat components.

Elevation, orientation, and associated climate are also important habitat variables for Denali's pollinators. Among the bumble bees, we know that species within the subgenus *Alpinobombus* (see above) are associated with northern latitudes and higher elevations, and the data confirm this, none were collected below 700 m (Table 2). In contrast, all the solitary bees were collected at lower elevations. Armbruster and Guinn (1989) note that Alaska solitary bees are most abundant and diverse in "open, sunny habitats at low elevations," especially on south-facing slopes and in early successional habitats such as floodplains and roads, but *not* in alpine areas. Because of their small body mass and lack of insulation, they must be able to bask in full sun either on the ground or in flowers, and they cannot tolerate the extreme thermal regimes that bumble bees do at higher elevations and in more shaded areas (Bishop and Armbruster 1999). Several of the flower flies I documented are considered northern or montane species (see next section), however they were almost all collected down to 550 m (Table 2). The unidentified *Platycheirus* sp. 7A and 7B showed a stronger relationship with elevation, all 52 specimens were collected between 935 and 1240 m. One relatively abundant flower fly, *Xylota notha*, whose larvae are associated with decaying wood, was found only at low elevations.

Potential and Current Threats to Pollinators

Insect pollinators are intimately linked to their host plants in complex ecological networks, and thus they may serve as effective indicators of ecosystem integrity. Identified threats to pollinators worldwide include habitat alteration and loss, pathogens, pesticides, invasive species, and a variety of effects associated with climate change (Potts et al. 2010). While pollinators in a protected wilderness like Denali may be less susceptible to many of these threats, effects from climate change are almost certain to confront species in this subarctic, high elevation system. Species in environments with compressed growing seasons and extreme climates have evolved a variety of complementary physiological adaptations and behaviors to survive such conditions, and thus responses to changes in temperature and moisture may be complex and difficult to predict (Danks 2004). One danger is that host plants and their pollinators will respond to climate change at different rates, so that the timing of flowering will no longer coincide with pollinator emergence. In a more temperate climate (northeastern U.S.), Bartomeus et al. (2011) looked to published phenology data on 10 solitary and bumble bee species and a number of known host plants, and concluded that phenological changes in bees had stayed in synch with parallel changes in plants over the past 130 years. However, this may not be the trend in climates with shorter growing seasons, or for bees with a narrower range of host plants. There is a growing body of research looking at effects of climate change on pollinator distribution and diversity in (sub)arctic and alpine systems (e.g., Dirnböck et al. 2011, Franzén and Öckinger 2012), and although results vary, one common conclusion among authors is that structured pollinator survey and monitoring on both local and global scales is imperative.

Bumble bees are the largest and most charismatic of the pollinators I surveyed in Denali, and their recent declines have received significant attention worldwide (Kosior et al. 2007, Goulson et al. 2008, Cameron et al. 2011). Williams et al. (2009) compared an assortment of species characteristics (e.g., body size, competition, food specialization) across bee faunas on three continents to determine which traits correlated most strongly with a species' susceptibility to decline. They concluded that bees at highest risk include species that are climate specialists and species that live close to the edge of their climatic range. Among Denali's bumble bees, we might expect that the species most susceptible to decline in the face of a changing climate would be those with circumpolar distributions, such as *Bombus hyperboreus* and *B. polaris*, and *B. neoboreus* restricted to sub/arctic North America (Table 2). Likewise, several of the flower flies I documented are specialists of northern latitudes, including *Cheilosia bigelowi*, *Eupeodes curtus*, and *Sericomyia nigra*. *Melangyna arctica* and *Parasyrphus tarsatus* are northern species that also extend south into Colorado and New Hampshire in alpine areas.

I collected a single specimen of *Bombus occidentalis* in Denali, a species known to be in dramatic decline further south in its range (Evans et al. 2008, Cameron et al. 2011). *B. occidentalis* was extremely common on the west coast of the U.S. until the mid-1990s, after which sightings dropped precipitously, despite intensive surveys (Evans et al. 2008). It is suspected that the primary cause for its decline was infection by a microsporidian fungus, *Nosema bombi*. In the late 1990s, *B. occidentalis* queens were sent to Europe for commercial rearing, and it is thought they picked up the pathogens there, from a related European bumble bee (Evans et al. 2008). Upon return to the U.S., the pathogens from the cultured bumble bees working in greenhouses, likely "spilled over" into surrounding wild bee populations from shared use of flowers (Colla et al. 2006). In Alaska, however, *B. occidentalis* appears to be quite widely distributed and abundant, Koch and Strange (2012) reported it from 14 of the 19 sites they surveyed for bumble bees along major highways of interior Alaska, from the Kenai Peninsula to well above the Arctic Circle. Additionally, the UAM database (http://arctos.database.museum; accessed 10/24/2013), shows 1,991 records for *B. occidentalis* collected by Pampell near USDA agricultural areas in 2009–2010 (Pampell 2010). Interestingly, despite the seemingly robust populations of *B. occidentalis* in Alaska, Koch and Strange (2012) found a high infection rate of *Nosema bombi* in the specimens they collected, and postulated that this may be an isolated North American strain of the pathogen that does not appear to be negatively affecting bee colonies. The single specimen of *B. occidentalis* I collected in Denali was found near the visitor center (site # 7). More surveys for this species in Denali would provide important information about the bee's status in subarctic habitats, though it is likely not common at higher elevations in the park (J. Strange, pers. comm.).

Educating Park Staff and Visitors about Denali's Pollinators

An important goal of the survey was to foster awareness and appreciation of insect pollinators to park staff and visitors. Denali's Wilderness boasts an impressive diversity of vertebrate fauna which visitors come to view and learn about from park staff, but, as in most national parks, the far vaster diversity of Denali's "microwilderness" has thus far received little attention (Rykken and Farrell 2013). In large part, this is because its small size makes it challenging to view, and because accessible information is scarce. Additionally, most insects evoke feelings of revulsion and/or fear among the general public, and a bee's potential to sting a visitor will likely receive more attention than its role as a pollinator in a complex ecosystem.

Engaging with the public at the visitor center and providing access to a microscope so that people could see the bizarre and beautiful attributes of pollinators up close, proved to be a successful way to generate curiosity and enthusiasm about Denali's "other fur bearers" (i.e., bumble bees) and their relatives. Setting bee bowls out on the path between the two visitor centers also intrigued and lured in visitors. Photo-rich presentations to the general public and park staff were well-received. Children are typically the most rapt audience for entomologists, and a half-day Denali-ology seminar provided local kids with an opportunity to collect as well as observe pollinators up close. Ideally, we will work on creating a field guide to common bees and flower flies of Denali, in addition to making fact sheets and web pages. Well-designed field guides encourage people to observe the world around them more closely, as they look for particular plants or animals. Another tool that is currently available to encourage visitors to observe and learn about native bees in Denali and elsewhere are Bee Observer Cards, available through the Encyclopedia of Life (http://eol.org/info/498).

Conclusions and Recommendations

This preliminary survey of Denali pollinators, although constrained by time and spatial coverage, establishes a baseline database for the diversity and distribution of two key pollinator groups, bees and flower flies. The fauna documented in the park thus far suggests that a diversity of bumble bees are key pollinators in all sampled habitats, foraging on a variety of plant hosts, but some species appear more strongly associated with higher elevations. Solitary bee species were found in only a few locations at lower elevations, but it is likely a higher diversity exists within the park, including more species in the Halictinae (e.g., *Lasioglossum*, *Halictus* species) as well as genera in the Megachilidae (e.g., *Osmia*, *Megachile*; Terry Griswold, pers. comm.). Flower flies were much more diverse than bees, and also occurred at a broad range of elevations, with a few species found primarily up higher.

Clearly, there is still much work to be done in Denali to gain a more comprehensive understanding of the current pollinator fauna, and also to prepare for monitoring changes in diversity, species composition, abundance, phenology, and range shifts over time.

Future priorities should include:

(1) Conduct additional basic survey work of bees and flower flies, with some modifications:

- Extend the sampling season from late May/early June to early August, to capture species that are active earlier and later in the season.
- Focus on documenting more solitary and cleptoparasitic bees, including targeting south-facing bluffs and slopes and lower elevation areas with potential nest sites (e.g., bare ground for nest-miners).
- Return to the East Fork Bridge and cabin area to find more specimens of the new *Cheilosia* flower fly species; begin to map its distribution in the park.
- Focus on netting pollinators (especially bees) directly from flowers, and keep track of host plant associations in a more structured manner.
- Run more bee bowl transects in alpine habitats (meadows and rocky areas) to capture the high elevation flower fly fauna more effectively.
- Sample streams and wetland edges more intensively, as well as shrub tundra and open taiga habitats.

(2) Begin an exploration of other dominant pollinators in the park, especially the non-syrphid flies (e.g., calypterates). As a start, facilitate the identification of the very abundant collections of bee bowl “by-catch” flies now stored in ethanol at UAM.

(3) Consider establishing a long-term pollinator monitoring program. Protocols could be fairly simple and run by volunteers, but such an effort would require connections with taxonomists, statisticians etc. Perhaps a regional Alaska monitoring effort which includes other parks would be more feasible.

(4) Continue to educate park staff and visitors about Denali's pollinators. A display case of bee and flower fly specimens in the MSLC visitor center, a field guide to common bumble bees, nest boxes at the visitor center for attracting cavity-nesting solitary bees, there are many possibilities!

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